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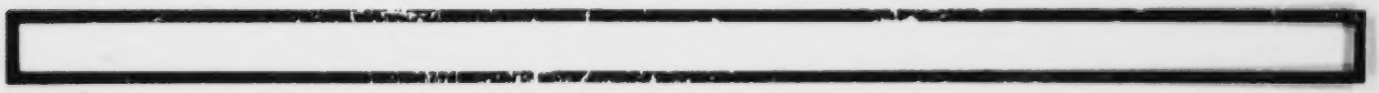

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by

James F. Heltshe and Nancy E. Forrester
University of Rhode Island
Kingston, RI 02881

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Estimating Species Richness Using the Jackknife Procedure

James F. Heltshe and Nancy E. Forrester[1]

Department of Computer Science and Experimental Statistics
University of Rhode Island, Kingston, RI 02881, U. S. A.

Summary

An exact expression is given for the jackknife estimate of the number of species in a community and its variance when one uses quadrat sampling procedures. The jackknife estimate is a function of the number of species that occur in one and only one quadrat. The variance of the number of species, and approximate two sided confidence intervals can be constructed. The behavior of the jackknife estimate as effected by quadrat size, sample size, and sampling area is looked at by simulation.

1. Introduction

The concept of diversity has been used in the last 30 years as a method for characterizing the structure of species abundance in a community. Certain characteristics are used to describe a biological collection: the number of individuals present in the community (N), the total number of species (S), and the proportion of abundance of each species (N_j, for $j=1,\ldots,S$, where $\sum_{j=1}^{s} N_j=N$). The diversity of collections small enough to be fully censused can be determined exactly without sampling error. However, for

[1]Present address:
E. C. Jordan Company
Portland, Maine

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indefinitely large communities, those too large for all members to be identified and counted, the diversity must be estimated from a sample of individuals; the estimate of diversity will then be subject to sampling error.

Taking a random sample of individuals is not easy to do in application. Kempton (1979) emphasizes that the theoretical standard errors for diversity values are inappropriate in nearly all cases, because they are derived from the assumption that repeated samples of fixed size are drawn from a homogeneous population, when, in fact, populations are inevitably heterogeneous in time and space. Pielou (1966) attempted to solve this sampling problem by taking repeated random samples of individuals and pool them together until the sample size is large enough to insure reasonable estimates. Smith and Grassle (1977) establish that given random samples of individuals, the Hurlburt (1971) expected species measure can be extended to nonhomogeneous populations. They show that the Hurlburt measure has an unbiased estimator, and they develop an unbiased estimator for its sampling variance.

When organisms have a continuum of space that they can occupy, there are no natural sampling units. The unit has to be arbitrarily defined, which suggests taking quadrat samples. Most biological communities demonstrate natural patchiness and clumping of species; consequently, samples drawn from natural communities are not random samples from a multinomial population (Smith and Grassle 1977). Samples taken are not random samples of individuals but random samples of space.

Extensions and modifications were applied to Pielou's (1966) pooled quadrat procedure (Lloyd, Inger and King, 1968, Heyer and Berven, 1973) but no new approach was attempted until Zahl (1977) applied the jackknife estimation technique to estimating species diversity indices.

We wish to focus our attention on estimating the oldest and most fundamental concept of diversity: the number of species in a community or species richness. This was the concept behind the formulatons of Fisher, Corbet, and Williams (1943) who first coined the term "diversity index". The difficulty with richness measure occurs when sampling from an infinite population. The larger the sample, the greater the expected number of species. The simplest, most practical, and objective measure of species richness is the direct species count of a sample. Some measurements of species/individuals relationships were proposed before popularization of the diversity concept (Gleason, 1922, Willis, 1922). Diversity indices of the richness variety have been proposed by Margalef (1957), Menhinick (1964) and Monk (1966). Most of these indices differ largely as a function of the number of individuals in the sample or population.

Calculating a species richness index from a sample presents a difficulty in that it is likely that several species in the population were missed in the sampling effort. The number of species found in a sample must be considered as a lower bound to the number of species in the population.

In Section 2 we derive the exact expression for the jackknife estimate of the number of species assuming a random sample of

quadrats. Section 3 gives some simulation results showing the behavior of the jackknife estimates. Section 4 contains an example of estimating the number of species in a benthic community.

2. Procedure

Suppose one has a random sample of n quadrats each of size a. For each quadrat, record presence/absence of each species found in that quadrat. The total species list will be based upon the pool of all n quadrats. The data is now in the form of Table 1.

Table 1

Presence (1)/absence (0) of species found in n quadrats

Species \ Quadrat	1	2	3	....	n
1	1	0	0	....	1
2	0	1	0		0
⋮	⋮				
S	1	1	1	....	1

Let $y^{o} = S$ be number of species found in pool of n quadrats.

$y^{-i}(i=1,2,\ldots,n)$ be the number of species found in pool of n-1 quadrats with ith quadrat removed.

$y_i(i=1,2,\ldots,n)$ be pseudo-value defined as

$$y_i = ny^{o} - (n-1)y^{-i}$$

f_j be the number of quadrats containing j "unique" species with

$$\sum_{j=0}^{s} f_j = n \text{ and } \sum_{j=0}^{s} jf_j = k$$

where k = total number of "unique" species in pool of n quadrats.

We define a "unique" species as a species that occurs in one and only one quadrat. A "unique" species will be represented by a row of Table 1 whose row total is 1. A "unique" species is a spatial rare species and not necessarily a numerically rare species. The jackknife estimate of the number of species is a function of these k "unique" species.

Since $y^{-i} = y^o$ if the ith quadrat contains no "unique" species; $y^{-i} = y^o - 1$ if the ith quadrat contains 1 "unique" species; $y^{-i} = y^o - 2$ if 2 "unique" species and so on; the pseudo values take on the following distinct values

$y_1 = y^o + j(n-1)$ where j is the number of "unique" species in quadrat i.

In summary

$$\begin{aligned} y_i &= y^o && \text{with frequency } f_o \\ &= y^o + (n-1) && \text{with frequency } f_1 \\ &= y^o + 2(n-1) && \text{with frequency } f_2 \\ &\vdots \\ &= y^o + j(n-1) && \text{with frequency } f_j \end{aligned}$$

It follows that the exact expression for the jackknife estimate of the number of species is

$$\hat{S} = (1/n) \sum_{1}^{n} y_i = (1/n) \sum_{o}^{s} f_j (y^o + j(n-1)).$$

$$= y^o + [(n-1)/n]k. \qquad (2.1)$$

$$\sum_{j=0}^{s} f_j = n \text{ and } \sum_{j=0}^{s} jf_j = k$$

where k = total number of "unique" species in pool of n quadrats.

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$$= y^o + [(n-1)/n]k. \qquad (2.1)$$

One can interpret this estimator as being a function of the k rare species. For every rare and "unique" species found in the sample, the jackknife estimate is (n-1)/n more than the total number found.

The variance of $\hat{S}$ can be found exactly to be

$$\mathrm{Var}(\hat{S}) = 1/(n(n-1)) \sum_{1}^{n} (y_i-\bar{y})^2$$

$$= \frac{n-1}{n} \left(\sum_{o}^{s} j^2 f_j - k^2/n\right). \qquad (2.2)$$

The variance of $\hat{S}$ takes on the following values

$$(n-1)/n[(k-k^2/n)] \leq \mathrm{Var}(\hat{S}) \leq (n-1)/n[(k^2-k^2/n)]. \qquad (2.3)$$

The lower limit is obtained when $\sum_{o}^{s} j^2 f_j = k$ or each of the k "unique" species occurs one per quadrat. The maximum is obtained if all k "unique" species are found in the same quadrat, then $\sum_{o}^{s} j^2 f_j = k^2$.

If one were to select a random sample of M individuals containing k singly occurring species, then the jackknife estimate of the number of species (jackknifed on groups of size 1) by Eq. 2.1 is

$$\hat{S} = y^o + \left(\frac{M-1}{M}\right)k$$

with

$$\mathrm{Var}(\hat{S}) = \frac{M-1}{M} [k-k^2/M].$$

3. Simulation Results

In order to study the behavior of the jackknife estimates of species richness when quadrat size and sample size are varied simulation is used. Four populations of approximately 5500 individuals were studied in the simulation experiments. Generated species proportions and population diversity values are given by Figure 1. The purpose of focusing on these populations was to examine the sensitivity of the Jackknife estimates to changes in distribution and species richness.

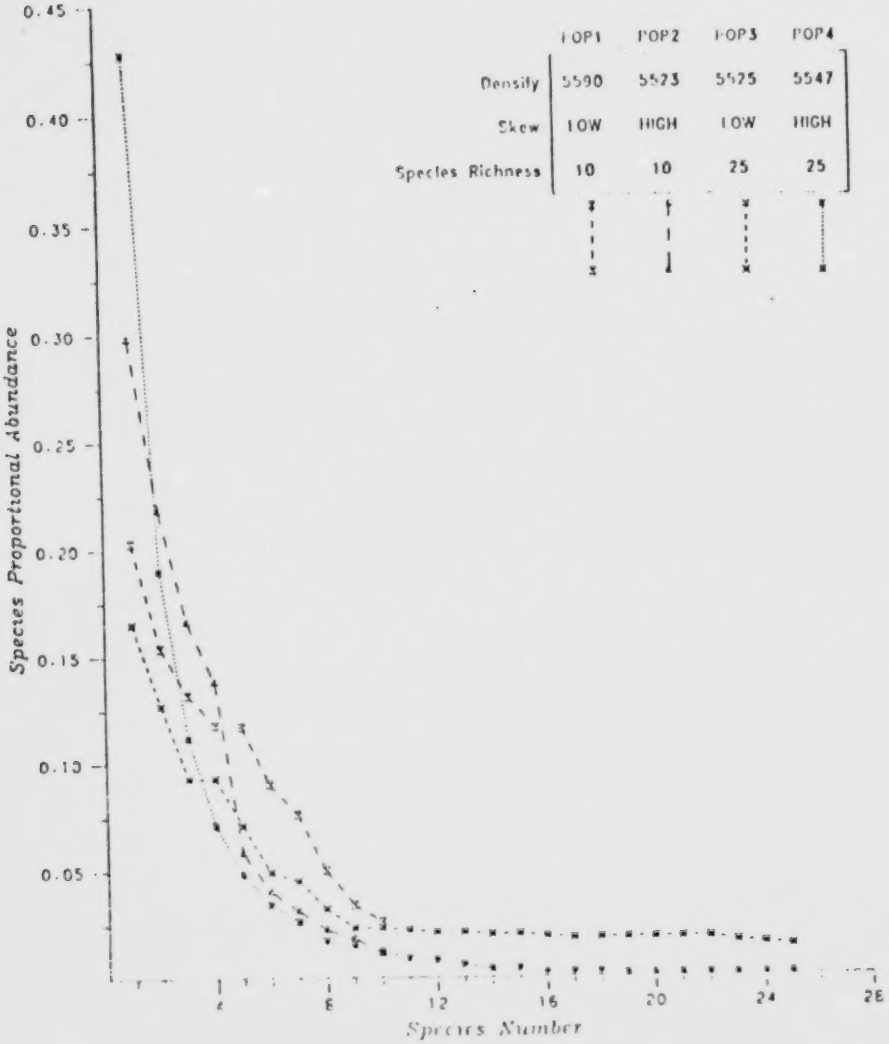
Monte Carlo simulation techniques were used to generate the four clumped populations using Diggle's (1976) "Modified Thomas Process". In generating our populations, it was desirable to create the natural patchiness and clumping of species that exist in most ecological communities. The study area is represented by a unit square in which 'parents' are randomly distributed, each parent then being surrounded by a clump of 'offspring'. A 'parent' coordinate pair (a,b) $0 \leq a,b \leq 1$, is selected by choosing two random values from the uniform distribution. For the jth species, the number of parents is generated as a Poisson variate with mean c_j, and for a given species abundance N_j, the number of 'offspring' for a parent is Poisson with mean λ_j where $\lambda_j = \sqrt{N_j/10}$. The square root transformation is made in order to reduce the variability in the number of offspring.

The average clump size for the jth species is $\lambda_j + 1$, the number of offspring plus the parent. The number of clumps for the jth species is actually equal to the number of 'parents' and

Figure 1. Distribution of species proportions for four simulated populations. Two populations with 10 species and 2 populations with 25 species. Low skew indicates low dominance on the part of 1 or 2 species, and high skew indicates high dominance and many rare species.

SPECIES ABUNDANCE DISTRIBUTION

for four populations



is calculated as $C_j = N_j/(\lambda_j+1)$. There will be more clumps of those species which occur in greater proportional abundance.

The offspring are spatially distributed about their parent in the following manner: the distance (r) of any offspring from its parent is distributed as a normal $(0,\sigma^2)$ distribution. The value of σ^2 defines the spatial clump size because approximately 95% of the individuals in the clump will lie within 2σ units of the clump's center. A value of $\sigma^2 = .02$ was chosen for this study in order to examine relatively tight clumping patterns. The direction (θ) from the parent to offspring is distributed uniform $(0,180°)$. The coordinates (x,y) of the new individual are found by the transformations; $x=a+r(\cos\theta)$, $y=b+r(\sin\theta)$, where (a,b) are the coordinates of the parent.

To study the effects of quadrat size, sample size, and sampling area an experimental design was set up as in Table 2. Entries in the table denote sample size.

Table 2

Experimental Design for Monte Carlo Simulation

Quadrat Size	Sampling Area 1	2	4
1	20	40	80
2	10	20	40
4	5	10	20

Increases in quadrat size represent doublings in area such that the smallest quadrat, 0.035 units per side, has an area of 1.25×10^{-3} square units, which is half the area of the medium size quadrat. With regard to spatial clump size, which is held fixed at 5.0×10^{-3} square units, the smallest quadrat would be 1/4 the size of the clump.

To examine the influence of sampling area on the jackknife diversity estimates, one looks across the rows of the table. Although sampling area, by its very nature, is confounded with sample size, the design permits fixing of quadrat size. By looking down the columns, it is possible to determine the effect of quadrat size. For fixed sample sizes, the effects of quadrat size confounded with sampling area are seen by focusing on the left to right diagonals of the table.

For the purposes of this study, empty quadrats (those which fall outside any clumps during the sampling) are discarded. In a diversity study that uses the jackknife technique, empty quadrats may artificially decrease the variance while adding nothing to the diversity of the community.

Tukey (1958) conjectured that the pseudo values obtained by the jackknife procedure can be treated as approximately independent, identically distributed, normal random variables, thus the jackknife method gives approximately normally distributed estimates. For this reason the goodness of the jackknife estimates was assessed by comparing observed confidence interval coverage as a function of quadrat size, sample size, and sampling area. Approximate 95% confidence intervals for the jackknife estimates are

$$\hat{S} \pm t_{n-1,\ \alpha/2}(\mathrm{Var}(\hat{S}))^{\frac{1}{2}},$$

where $\hat{S}$ and $\mathrm{Var}(\hat{S})$ are obtained from equations 2.1 and 2.2 respectively. Results are based upon 100 realizations of the sampling combinations of Table 2. Jackknife estimates, percentage cover of confidence intervals, and mean confidence interval length are given for each sampling combination.

Table 3 gives the results of the jackknife estimation of species richness for the populations with 10 species (low and high skew, respectively). Behavior of the jackknifed index is good for both populations, in spite of distributional differences, and the percentage cover of the two-sided 95% confidence intervals is generally high in all cases. For fixed quadrat sizes coverage increases and mean confidence interval length becomes narrower as sample size (thus sampling area) increases. When the sampling area is fixed any appreciable increase in observed coverage is obtained at the expense of increased interval length as quadrat size increases. Wider confidence intervals with larger quadrats are due in part to increased natural variability that occurs with smaller sample sizes, but also to sampling variability, which depends on the spatial location of quadrats relative to clumps. For example, a small quadrat, only 1/4 the size of a clump, will tend to fall either in the middle of a clump, and thus contain a large number of individuals, or wholly outside a clump. Large quadrats, on the other hand, may cut through part of a clump and remain largely empty. As a result larger numbers of unique species are detected in the larger quadrats. The species richness estimate as discussed in Section 2 is a

function of the number of unique species. Differences which appear because of changes in skewness do not change conclusions about the effect of quadrat size and sample size. Minimum confidence interval length and maximum percentage cover indicate that a large number of small quadrats provide the best representation of the community. For fixed sample sizes, more precise and accurate estimates were obtained by sampling larger areas, thus using larger quadrats.

[Table 3 goes here.]

When the number of species was increased from 10 to 25, the behavior of the jackknifed species richness index became more interesting. The results of the jackknifed estimation for the two populations are given by Table 4. The percentage cover and other sample statistics indicate that the jackknife estimate of species richness is sensitive to the number of common species in the population as much as to the number of rare species. Although standard errors and mean confidence interval lengths are higher, percentage cover for the lower skewed population is essentially similar to the coverage for the two populations with 10 species. Coverage is very poor for the highly skewed population and the mean confidence interval lengths remain erratically high regardless of sample size or quadrat size. Because the number of species obtained in a sample is always the lower bound of the number of species in a community, jackknife estimation underestimates the number of species when there are a large number of rare species in the community.

Species Richness Jackknife Estimates

S = 10

Sampling Area (units squared)

Quadrat Size	A_1 .025 Low	A_1 .025 High	A_2 .050 Low	A_2 .050 High	A_3 .100 Low	A_3 .100 High
		20		40		80
$(.035)^2$	10.4 2.59 87%	10.7 4.55 85%	10.1 0.47 95%	10.4 2.18 89%	10.0 0.04 100%	10.1 0.51 100%
		10		20		40
$(.050)^2$	10.7 4.04 84%	10.6 5.38 89%	10.2 1.25 94%	10.5 3.06 84%	10.0 0.00 100%	10.1 0.71 93%
		5		10		20
$(.071)^2$	10.8 5.89 92%	10.1 6.42 93%	10.3 2.11 89%	10.6 4.35 87%	10.0 0.24 99%	10.3 1.25 94%

Skew

Low High

	n
J.K. CI Length % Cov.	

Values are means of 100 trials and are given for both low and high skewed distributions.

J.K.: mean jackknife value
CI Length: mean confidence interval length
% Cov.: observed CI coverage for 100 trials
n: sample size

Table 4

Species Richness Jackknife Estimates

S = 25

Quadrat Size	Sampling Area (units squared) A_1 .025 Low	A_1 .025 High	A_2 .050 Low	A_2 .050 High	A_3 .100 Low	A_3 .100 High
$(.035)^2$	n = 20		n = 40		n = 80	
	J.K. 26.7	16.5	26.8	20.3	25.2	23.4
	CI Length 10.06	8.03	6.42	8.22	1.04	8.22
	% Cov. 84%	14%	86%	43%	96%	75%
$(.050)^2$	n = 10		n = 20		n = 40	
	J.K. 26.4	15.7	27.1	19.0	25.5	22.7
	CI Length 10.93	8.01	7.84	8.25	2.06	8.12
	% Cov. 85%	9%	84%	30%	90%	68%
$(.071)^2$	n = 5		n = 10		n = 20	
	J.K. 25.0	14.7	27.3	19.0	26.0	22.6
	CI Length 12.50	9.29	8.98	8.91	3.75	8.47
	% Cov. 86%	5%	85%	35%	89%	61%

Skew: Low / High

n

J.K.
CI Length
% Cov.

Values are means of 100 trials and are given for both low and high skewed distribution.

J.K.: mean jackknife value
CI Length: mean confidence interval length
% Cov.: observed CI coverage for 100 trials
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4. Example

As an illustration of the procedure developed in Section 2 we will apply equations 2.1 and 2.2 to the data in Table 5. This is a benthic infaunal sample of a subtidal marsh creek collected in April 1978 in the Pettaquamscutt River in Southern Rhode Island by Jeffrey Hyland of the Graduate School of Oceanography of the University of Rhode Island.

[Table 5 goes here.]

Circled values indicate "unique" occurrences of species, i.e. they occur in one and only one column (quadrat). For this example $f_0=6$, $f_1=3$, and $f_2=1$, the number of quadrats with 0, 1, 2, "unique" species, $k = \sum_{0}^{s} jf_j = 5$ and from equations 2.1 and 2.2 we get

$$\hat{S} = 14 + (9/10)5 = 18.5$$

$$\text{Var}(\hat{S}) = 9/10\ (3+4 - 25/10) = 4.05$$

with the two sided approximate 95% confidence interval being

13.95 to 23.05.

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Table 5. Sample taken from a subtidal march creek, April 1978
Pettequamscutt River, Rhode Island

Species List	Quadrat Number 1	2	3	4	5	6	7	8	9	10
Streblospio benedicti		13	21	14	5	22	13	4	4	27
Nereis succines	2	2	4	4	1	1	1		1	6
Polydora ligni		1						1		
Scoloplos robustus	1		1	2		6			1	2
Etoone heteropoda			1	2			1			1
Heteromastus filiformis	1	1	2	1		1			1	5
Capitella capitata	(1)									
Scolecolepides viridis	(2)									
Hypaniola grayi		(1)								
Branis clavata			(1)							
Macoma balthica			3							2
Ampelisca abdita			5	1		2				3
Neopanope texana								(1)		
Tubificoodies sp.	8	36	14	19	3	22	6	8	5	41

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